Examensarbeten 2014:21

Fakulteten för skogsvetenskap
Institutionen för skogens ekologi och skötsel

Effect of planting density and abiotic conditions on yield of *Betula pendula* and *Pinus sylvestris* seedlings in monoculture and mixture

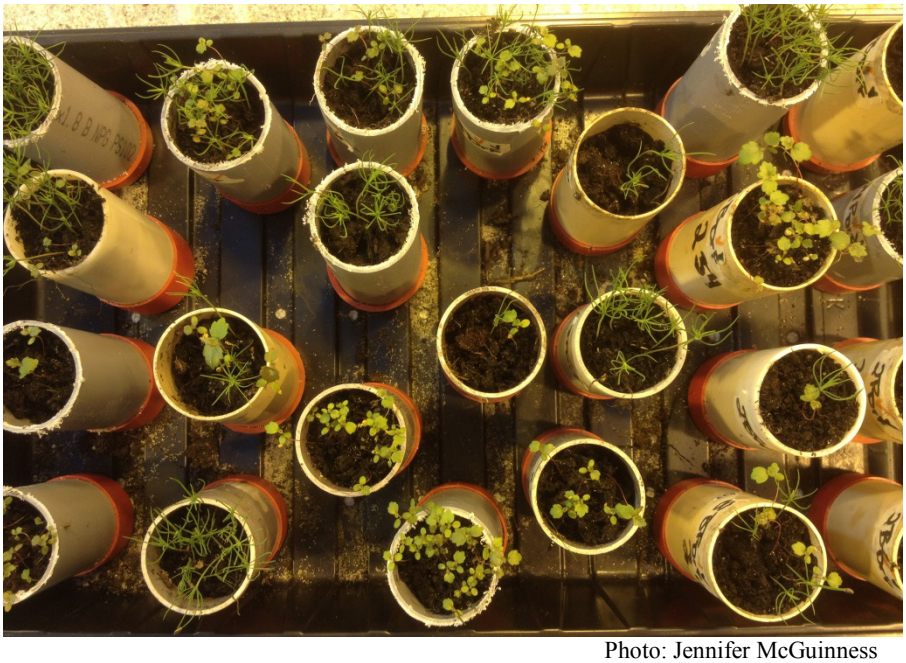

Photo: Jennifer McGuinness

Jennifer McGuinness

Sveriges Lantbruksuniversitet
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I denna rapport redovisas ett examensarbete utfört vid Institutionen för skogens ekologi och skötsel, Skogsvetenskapliga fakulteten, SLU. Arbetet har handletts och granskats av handledaren, och godkänts av examinator. För rapportens slutliga innehåll är dock författaren ensam ansvarig.

This report presents an MSc/BSc thesis at the Department of Forest Ecology and Management, Faculty of Forest Sciences, SLU. The work has been supervised and reviewed by the supervisor, and been approved by the examiner. However, the author is the sole responsible for the content.

Abstract

How the yield of mature stands changes in response to factors such as stand composition, planting density and abiotic conditions is a developing topic, and underpins models and generalizations used by forest managers today. However, these generalizations are both the subject of debate and are limited to mature stands, leaving a knowledge gap concerning both mixed species stands and younger stands. I performed this study to address this knowledge gap. Using seedlings of two common boreal tree species (*Betula pendula* Roth and *Pinus sylvestris* L.), three planting compositions (two monocultures and one 50:50 mixture), four planting densities (2, 8, 16 and 24 seedlings per pot) and four abiotic conditions (high nutrient + high water, high nutrient + low water, low nutrient + high water and low nutrient + low water) I tested the effects of these factors on the yield characteristics of seedlings.

Under greenhouse conditions seedlings were grown for 10 weeks in a full factorial block design experiment. Total seedling masses, mean seedling masses, above and below ground (A:B) masses, A:B ratio, mortality, height and diameter were measured to observe if changes in seedling yield characteristics occurred. My results show that seedling yield is affected by all three factors; species composition, density and abiotic environment, as well as interactions among them. The significant interaction terms indicated not only that the seedling performance differed among planting compositions (e.g. between seedling monocultures and mixtures), but that the effects were also dependent on both the planting density and the abiotic conditions. Total mass, above ground mass and below ground mass of monocultures and mixed planting composition significantly increased with increased density in all planting compositions. While mean seedling mass, and seedling diameter showed significant decrease with increasing density. While often not statistically significant the change in seedling performance of each planting composition with increasing density var-

ied with abiotic conditions. Under conditions of high nutrient + high water an overyielding effect is observed, notably at intermediate planting densities. However, yield in mixtures was only significantly different from birch monocultures. When mean seedling mass was plotted on a log mass - log density scale the observed relationships were all negative but varied in intensity, when planting composition and abiotic conditions were changed refuting the self thinning rule and proposed constant slope. The results from this experiment suggest that these three factors and their interactions influence yield in seedlings, and that overyielding may occur under specific conditions. These results also contribute to the debate on the general applicability of the self-thinning law, by showing that the relationship between yield and density is not constant. Such findings contribute to the understanding of yield and the effects of stand characteristics on seedling performance.

Keywords: Abiotic environment, Betula pendula, Density gradient, Interaction effects Pinus sylvestris¸ Planting density, Planting composition, Seedling yield.

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1 Introduction

Stand structure and tree species composition are key attributes of forest ecosystems, and are determinants of total stand yield (Griess and Knoke, 2011). A great deal of effort has been put into developing a thorough understanding of how stand composition, population density, and abiotic conditions impact on total yield of forests (Skovsgaard and Vanclay, 2008, Pretzsch, 2009) as well as how these factors impact on forest production (Cater and Chapin, 2000, Skovsgaard and Vanclay, 2008, Treberg and Turkington, 2010, Griess and Knoke, 2011, del Río et al., 2014). For example, numerous studies have investigated how density-dependent growth of entire stand communities including understory vegetation and canopy cover trees varies with soil resource availability (Treberg and Turkington, 2010), and how total yield is impacted by density-dependent factors, such as resource competition and species interactions, that increase with crowding (Condes et al., 2013). Many of these studies are developed from uniform mono-specific mid rotation aged stands, and recently more studies addressing how these relationships apply for stands of multiple species are being published (see Kelty (1992), Frivold and Frank (2002), Kelty (2006), Condes et al. (2013), Gamfeldt et al. (2013), Lundqvist et al. (2014)). The development of silvicultural systems that

maximize yield of monocultures has led to the conversion of once highly diverse European forest stands into monospecific conifer stands (Bjorse and Bradshaw, 1998, Farrell et al., 2000). This has in turn raised concern of the reduction of species richness and brought attention to the effects of forest diversity (Hooper et al., 2005). How forest diversity may impact on forest ecosystem productivity and total yield is therefore widely debated (Gamfeldt et al., 2013). Some authors present evidence that mixed species stands are more productive than monocultures (Condes et al., 2013, Kawaletz et al., 2013) or may better resist catastrophic events (such as storms) and predicted climate change (Drobyshev et al., 2013). However, there is limited understanding and agreement regarding the potential benefits of species mixing in practical forestry (Agestam et al., 2006).

Stand growth is regulated by a variety of factors, of which species identity, resource availability and population densities are considered to be among the most important (Pretzsch, 2009). The current body of literature on stand yield is based predominantly on past and present field observations of mature forest stands, and has led to varied results as to whether or not mixed stands are superior to monospecific stands. For example, a review of previous studies by Pretzsch et al. (2010), showed that overyielding often occurred as the result of stand mixing in central European stands of Norwegian spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* L.). Additionally, Hynynen et al. (2011) found that yield in mature mid rotational stands of southern Finland changed with the proportion of each species within the stand and decreased as the ratio of silver birch (*Betula pendula* Roth) to Scots pine (*Pinus sylvestris* L.) increased. In contrast, Pretzsch et al. (2012) concluded that the potential for overyielding in the mixed

stand varied with the environment as opposed to the species mixture ratio. It is unclear based on available evidence as to how mixed stands perform relative to single species stands (Pretzsch et al., 2012). The inconclusive nature of present evidence could be due to various factors that may differ among studies; notably species compositions, resource availability, measures of and account for tree interactions (Hooper et al., 2005). Furthermore, the regional and local climate, stand density, stand age, stand management and individual tree characteristics are not constant between studies and therefore contribute to the contradictory results (Pretzsch et al., 2012).

While the precise development of a stand is subject to many factors it is generally assumed that the relative growth and biomass accumulation of tree populations becomes less when the stand reaches maturity, possibly due to finite resource availability and increasing volume (Pretzsch, 2002). As the stand develops, each individual tree within the stand consumes more resources until crown closure or critical density levels are reached. Once this level of stand maturity is reached density-dependent growth effects start to emerge and competition effects begin to show in the growth and survival of the population (He and Duncan, 2000). Early observations of the basic relationship between density and total yield of monocultural even aged stands by Reineke (1933) and Yoda et al. (1963) led to the development of a model which predicted stand yield, biomass (B) or weight (m), based on stand density (N). This relationship is also known as the -3/2 power law or the self-thinning rule (Pretzsch, 2002). As an empirically based rule, it predicts that the relationship between size and density in an even aged mono-specific stand can be determined as the logarithm of average mass plotted against the logarithm of

plant density, with the resulting straight line as the 'self-thinning line' (Weller, 1987). When the population increases above a critical density, self-thinning or density dependent mortality occurs (Lonsdale, 1990). This self-thinning rule is represented by the basic equation:

$B = kN^{(-a)}$ or $\log B = (a) \log N + \log k.$

Where B is the stand biomass, k and a are constants and N is the stand density (Lonsdale, 1990). According to allometric observations and modeling of even aged single plant species, it is estimated that a, a species invariant scaling exponent, should be approximately -3/2 (Lonsdale, 1990, Zeide, 2010, Weller, 1987, 1979, Pretzsch, 2009). This rule has been often reviewed, adapted and debated; it was for long considered a universal relationship, but many studies have also refuted its generality (Weller, 1987, Lonsdale, 1990, Charru et al., 2012). Moreover there is a lack of development of this type of relationship in mixed stands, leaving a knowledge gap and limited applicable knowledge for use in stand management. This gap has been cited as a potential reason for the limited use of mixed stands in practical forestry today (Treberg and Turkington, 2010). Although highly debated, the general understanding of the self-thinning rule has been frequently used by forest managers to determine the optimal thinning regimes and to predict natural mortality (Vanclay and Sands, 2009). As such, further investigation is needed to assess how well the self-thinning rule is applicable in a given stage of stand development for different stand compositions (Treberg and Turkington, 2010).

The majority of studies investigating over-yielding and density-dependent growth relationships are from mature stands, and there is a lack of studies addressing this issue for boreal saplings and seedlings. As early stages of tree establish-

ment are strongly influenced by growing conditions in different ways than mature stands (Ponge et al., 1998), it is expected that seedlings will respond differently to stand conditions (density, composition and resource availability) than the equivalent mature stand. It is also suggested that responses to planting density of seedlings will differ from those seen in mature stands, which would cause seedling self-thinning curves to differ from the suggested self-thinning law (Charru et al., 2012). Using two common native boreal and commercially important tree species in Sweden, *Pinus sylvestris* (Scots pine) and *Betula pendula* (Silver birch) (Frivold and Frank, 2002), I performed a full factorial 10-week greenhouse experiment to develop a better understanding of how seedling yield in mixtures differs from that in monocultures under different density and environmental conditions. This study contributes to the advanced understanding of density dependent growth in seedling mixtures and monocultures under different abiotic conditions, and further if species in mixture could alleviate reductions in seedling performance expected with modified abiotic conditions. Specifically, I intend to address the following questions: (1) Is there a difference in final seedling performance between tree seedling planting compositions and is this affected by planting density? (2) Is there an effect on final seedling biomass yield by density and does it differ under different abiotic conditions? and (3) Are there differing effects on final seedling yield by planting composition in different environments? By testing for these questions I seek to also review the nature of the self-thinning rule and how the curve-linear relationship between density and plant biomass yield in seedlings may vary between monocultures and mixtures as well as under adverse environmental conditions.

2 Materials and Methods

2.1 Experimental design

In order to examine how tree species composition and density affect total biomass yield and how this relationship is modified by different abiotic conditions, I established a full factorial standard replacement series in which different densities of tree seedlings were grown in pots in a greenhouse in monocultures and polyculture under two levels of moisture and fertility. The experiment consisted of 48 treatment combinations; three seedling combinations (*B. pendula* in monoculture, *P. sylvestris* in monoculture, and *B. pendula* plus *P. sylvestris* mixture), four planting densities (a total of 2, 8, 16 or 24 seedlings per pot, with these total densities maintained in both monocultures and mixtures), and four growing conditions consisting of high and low nutrient soils fully crossed with two levels of water additions. A total of 5 replicates of the 48 different treatments and treatment combinations were established in a randomized complete block design resulting in 240 experimental units. Each unit (hereafter 'experimental unit') was composed of prescribed growing medium (see below) and seedlings within a 200 cm^3 (2.5 cm radius by 10 cm height) cylindrical opaque plastic pvc tube. *B. pendula* and *P.*

sylvestris seedlings were planted in monocultures at each of the four densities as well as in a 1:1 species: species s combinations using a substitutive replacement series design (Freckleton and Watkinson, 2000). This involved that for each of the four densities, seedlings in the mixture had the same total density as the species in the corresponding monocultures. By using this design I expected to be able to compare and contrast the differences from imposed experimental treatments between the monocultures and the mixture. The design was chosen for the ability to manipulate the components in a continuous range of densities, despite the inability to distinguish between inter-and intra-species competition effects (Freckleton and Watkinson, 2000).

2.2 Growing medium

The growing medium was prepared as three soil layers to mimic natural soil horizons (Rothe and Binkley, 2001)(Figure 1). First, all experimental units were filled at the bottom with 3-cm of a mixed base layer of industrial quartz sand and Hasselfors K-jord soil, in a 2:1 volume to volume ratio to allow for drainage (Figure 1). On top of this layer, 3 cm of a 2:1 mix of natural mineral soil: Hasselfors K-jord was added allowing for drainage and incorporation of natural soil nutrients and biota. Lastly a top layer was added consisting of 3 cm of either (a) a 1:1 mixture of natural humus: Hasselfors K-jord (hereafter high nutrient) or (b) a 14:1 mixture of natural humus:Hasselfors K-jord (hereafter low nutrient). By using two different growth medium mixtures for the top layer I imposed a nutrient treatment, with two soils that differed in fertility, notably macro nutrients, thus representing

contrasting conditions likely to be found on spot scarified clear-cuts prior to seeding or planting. All natural soil materials, humus and mineral substrates, were collected from a 2 year old harvested *P. sylvestris* stand in Bergsboda, Sweden (63°46'N, 20°20'E) in November, 2013 prior to ground freeze. Both mineral and humus collected materials were cleaned of all large woody debris, stones and green living plant material, then stored separately until the experimental units were prepared. Hasselfors K-jord is a potting mix, consisting of 95 % light peat (2-30 mm white H2-4 humification) and 5 % sand. The mix has a pH of 6.0, density of 340 kg/m^3, >60% organic matter content, and N:P:K 14:7:15 (Holmberg, 2014).

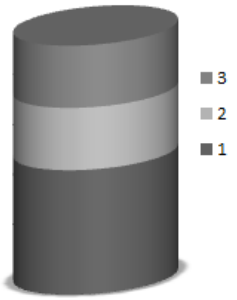

Figure 1. Growing substrate layers within experimental units. *Layer 1* -industrial quartz sand and Hasselfors K-jord mixture (2:1 volume/volume ratio); *layer 2* -mixed natural mineral soil and Hasselfors K-jord mix (2:1 v/v), and; *layer 3* -either a 1:1 or a 14:1 mix (v/v) of collected humus and Hasselfors K-jord. (Not to scale)

2.3 Seedlings

Seeds of *B. pendula* and *P. sylvestris* were pre-germinated on cleaned coarse grained industrial quartz sand watered to field capacity under artificial light at room temperature (Nilsson and Zackrisson, 1992). These species were selected on the basis that mixed forests in Scandinavia are most often *B. pendula* admixtures in *B. pendula* or *Picea abies* (Norway spruce) dominated stands (Hynynen et al.,

2011). *B. pendula* and *P. sylvestris* are both early successional species which may enhance effects in the mixed species planting composition within the short 10 week growing period. The use of early successional species has been cited as a practical method to examine the life history during the seed to sapling life stages (Dalling and Hubbell, 2002). However, both species have differing niches (notably stress responses, and resource use) and as such have differing site requirements and reactions to disturbance. *B. pendula* is generally more common in naturally regenerating sites of higher fertility relative to *P. sylvestris* and is often found on mid to high points within pine stands, whereas *P. sylvestris* is more common in sites of poor fertility or moisture (Frivold and Frank, 2002). By having two species with different niches, I maximized the potential for differences between site conditions and any effect in the mixed species planting composition may be greater.

After germination, seedlings were left to grow for approximately 18 days until primary needles and leaves had developed and stems were strong enough to undergo transplanting. Minimal amounts of a weak N:P:K fertilizer was applied to enhance initial growth as per manufacturer dosage. Seedlings were planted to establish a density gradient for the density treatment. In monoculture treatments, each experimental unit was planted with 2, 8, 16 or 24 seedlings of *B. pendula* or *P. sylvestris* in rows within each pot maintaining equal space between seedlings across all treatment densities. In mixed treatments seedlings of *B. pendula* and *P. sylvestris* were planted in rows with the two species planted in alternating postions and in a 1:1 proportion across the four densities (Figure 2). A total of 750 seedlings were initially planted into a total of 240 units for the 5 replicates used.

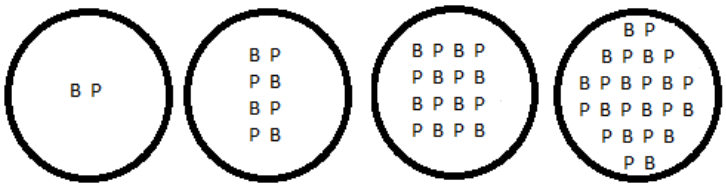

Figure 2. Planting configuration, showing mixed species alternating pattern and equal spacing distance between seedlings. (Not to scale)

All units were left to acclimatize for a period of 2 weeks in the greenhouse until the moisture treatment was applied. This involved establishing units of limited moisture by amending these units with 50% of the volume of water added to non-limited units as done by Agestam et al. (2005) with the moisture limited units receiving the minimal amount of water to maintain growth (e.g. 25 ml vs 12.5 ml). All units were watered every second day. Replicate blocks were rotated systematically within the greenhouse over the course of the study to reduce impact from variation in environmental conditions in the greenhouse. Greenhouse conditions throughout the experiment were maintained with 18 hours of light, relative humidity of 60 ± 10 %Rh and daytime and night time temperatures of 20˚C and 15˚C respectively. Misting spray for maintaining the relative humidity was directed away from the planted pots to limit influence on moisture treatments. Throughout the growth period units were cleared of various bryophyte species that established from spores on the humus surface. Planted seedlings were left to grow with applied treatments for a period of 10 weeks.

2.4 Harvesting and measurements

The initial biomass differed between *B. pendula* and *P. sylvestris* seedlings and to avoid possible bias comparing mass between two species of different size

(Freckleton and Watkinson, 2000) 100 random seedlings of *B. pendula* and *P. sylvestris*, respectively, were selected from the pre-germinated batches at the time of planting (i.e., after 18 days of germination on sand). These were oven dried over 24 hours at 60°C, weighed to determine the initial mean mass per seedling and then used in calculating the final yields. *B. pendula* seedlings weighed on average 0.0024 (± 0.002 SE) g and *P. sylvestris* on average 0.0063 (±0,006 SE) g seedling^{-1}. Following 70 days of growth with applied treatments, height, diameter and species identity of the tallest seedling in each pot regardless of species was recorded before seedlings were harvested sequentially by replicate (Dehlin et al., 2004). Seedlings were removed from the pots, roots were carefully hand washed to remove soil, and plants then divided into above ground biomass and below ground biomass. The above ground and below ground biomass of the seedlings was oven dried for 24 hours at 60 °C and weighed separately. Using the dry weights the above: below ground biomass (A:B) ratio was determined for each experimental unit. To determine treatment mortality, the number of dead seedlings per pot and their species identity was recorded; total percent mortality per pot was determined to depict survival across all treatments.

2.5 Statistical analysis

I analyzed all response variables using a full factorial general linear model (GLM) performed with Minitab® 16 Statistical Software (MinitabInc., 2013). I used planting composition (i.e. monocultures of *B. pendula* and *P. sylvestris* or the 1:1 mixture), planting density and environment as fixed factors and block as a random

factor to determine statistically significant effects of the factors and their interactions on the dependent variables. The dependent variables included total biomass, above ground biomass, below ground biomass, A:B ratio, individual seedling mass (total mass/ planting density), maximum seedling height, diameter of tallest seedling, and mortality. First I tested for normality of distribution, using graphic probability plots and Levene's test of equal variance (Minitab Inc., 2013). Where needed (i.e., for A: B ratio, mortality and individual seedling mass) data was log transformed to satisfy the model assumptions of normal distribution and equal variance.

In all statistical analyses a 95 % confidence level was used (i.e. $\alpha = 0.05$) to test null hypothesis stating that all means are equal ($H_o : \beta_i = 0$) against the alternative hypothesis, means are not equal ($H_a : \beta_i \neq 0$). Significant results, showing difference between the means, were recorded where a p-value was lower than the $\alpha = 0.05$ confidence limit. Where significant effects of factors were detected in the GLM, a post hoc test was performed to explore differences among means. The test I used was Tukey's HSD with a family error rate of 0.05 (Minitab Inc., 2013). Where log transformations were performed I used antilog transformations to return data to enable graphic depiction.

Lastly I reported and commented on the yield-density relationship of each planting composition under each of the four different environments.

3 Results

3.1 Main Treatment Effects

3.1.1 Composition

Seedling planting composition had significant effects on total biomass, below ground mass, above: below ground (A:B) mass ratio, mortality and mean seedling mass per pot, while above ground mass and diameter were not significantly affected (Table 1). The *P. sylvestris* monocultures resulted in greater total biomasses than the mixed species planting compositions and the *B. pendula* monocultures, with the mixed species composition resulting in intermediate total biomasses (Figure 3). The composition effect on mean seedling mass was similar to that of total mass, with the greatest mean mass in *P. sylvestris* monocultures and the lowest mass in *B. pendula* monocultures, while the mixed species planting composition again resulted in intermediate biomasses (Figure 4). The A:B ratio was significantly lower in *P. sylvestris* monocultures than either the mixed species planting composition or the *B. pendula* monocultures (Figure 5). Similar to the total mass and mean seedling mass, the mixed species planting composition resulted in interme-

diate values while *B. pendula* monocultures resulted in the greatest A:B ratio (Figure 5). The difference in A:B ratio between planting compositions was supported by the significant effect of composition on below ground masses (Table 1). As such, *P. sylvestris* monocultures clearly had the greatest below ground mass, the mixed species composition had intermediate below ground mass values and *B. pendula* monocultures had the lowest below ground mass (Figure 6). The planting composition also had a significant effect on seedling mortality (Table 1), with *B. pendula* monocultures presenting the highest mortality, *P. sylvestris* monocultures the least, and the mixed planting composition presenting values for mortality in between both monocultures (Figure 7).

Table 1. The effects of manipulated variables; planting composition (*Betula pendula* in monocultures, *Pinus sylvestris* in monocultures, or *Betula pendula* and *Pinus sylvestris* in polyculture), planting density and abiotic environmental conditions and their interaction effects on seedling biomass yield and yield characteristics). Values represent the results (F-value) of a three-way ANOVA with block as a random factor and significant levels (p-values) in parentheses. Significant effects are shown in bold ($p < 0.05$).

Response variable	Total biomass	Above ground biomass	Below ground biomass	Above: below ground mass ratio*	Mortality*	Mean seedling mass*	Diameter
Composition (C)	**16.71 (<0.001)**	0.02 (0.982)	**129.90 (<0.001)**	**21.83 (<0.001)**	**17.29 (<0.001)**	**14.24 (<0.001)**	1.49 (0.229)
Density (D)	**29.98 (<0.001)**	1.41 (0.241)	**146.10 (<0.001)**	**13.22 (<0.001)**	**32.83 (<0.001)**	**154.43 (<0.001)**	**11.31 (<0.001)**
Environment (E)	**4.21 (0.007)**	1.26 (0.288)	**8.97 (<0.001)**	0.06 (0.982)	1.82 (0.145)	**4.05 (0.008)**	**10.98 (<0.001)**
C x D	1.45 (0.196)	0.87 (0.517)	**24.54 (<0.001)**	**3.20 (0.006)**	2.09 (0.057)	0.62 (0.713)	**2.75 (0.014)**
C x E	**4.40 (<0.001)**	**4.99 (<0.001)**	0.37 (0.900)	3.16 (0.376)	0.84 (0.543)	**2.30 (0.036)**	**2.68 (0.016)**
D x E	0.63 (0.773)	0.92 (0.513)	1.01 (0.437)	**1.08 (0.013)**	0.89 (0.537)	1.30 (0.237)	0.72 (0.692)
C x D x E	3.47 (0.124)	**2.10 (0.007)**	0.56 (0.927)	1.97 (0.14)	0.91 (0.565)	1.12 (0.34)	0.45 (0.975)
Block	**3.47 (0.009)**	0.25 (0.907)	**18.52 (<0.001)**	**1.75 (0.005)**	0.31 (0.87)	1.36 (0.249)	**13.55 (<0.001)**

Environment: Df= 3, F_{crit}: 2.64 Density: Df= 3, F_{crit}: 2.64; Composition: Df= 2, F_{crit}: 3.03; Environment x density: Df= 9, F_{crit}: 1.91; Environment x composition: Df= 6, F_{crit}: 2.13; Density x composition: Df= 6, F_{crit}: 2.13; Environment x density x composition: Df= 18, F_{crit}: 1.64; Block: Df= 4, F_{crit}: 2.40; residuals: Df = 188.

* Data are log transformed

3.1.2 Density

Total seedling mass, mean seedling mass, A: B ratio, and below ground mass per pot, as well as the diameter of the tallest seedling were significantly affected by planting density, and only above ground mass was unaffected (Table 1). When planting density increased from 2 seedlings to 24 seedlings per pot, both total mass (Figure 3), and below ground mass (Figure 6) significantly increased. Mean seedling mass showed the opposite pattern and significantly decreased with increasing density (Table 1, Figure 4 and 8), as revealed by the negative slope value for all regression lines of the log biomass- log density relationship (Table 2). Increasing density also significantly reduced the A:B ratio, however, this effect of density was weaker than for the other mass variables and showed a minor decline in ratio with increased density (Figure 5). This was also true for the diameter of the tallest seedling, which showed only a slight observable decline with increasing density (Figure 8).

3.1.3 Environment

The abiotic environment had significant effects on total seedling mass, mean seedling mass, below ground mass and seedling diameter while above ground mass, A:B ratio and mortality were unaffected (Table 1). Under conditions of low nutrients (irrespectively of water), total seedling mass was the lowest (Figure 3); this was exacerbated when both nutrients and water were decreased. When water was reduced irrespective of nutrients, in general total mass was only marginally lower in low nutrient conditions compared to high nutrient condition or showed no response (Figure 3). Below ground mass was significantly greater in conditions of high nutrients irrespective of water conditions. Under conditions of low nutrient +

low water the below ground mass was marginally lower than under conditions of low nutrient + high water (Figure 6).

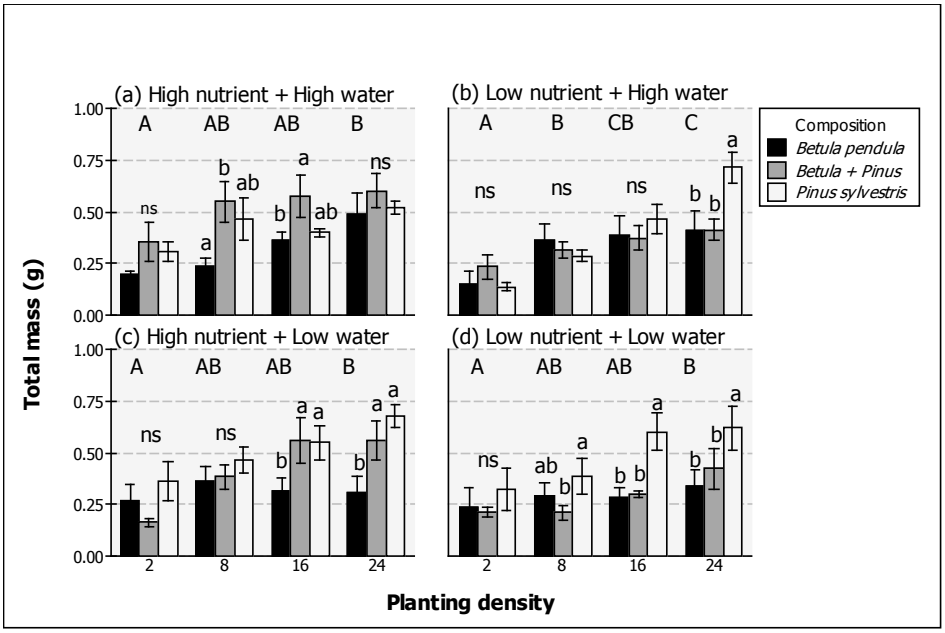

Figure 3. Total mass (g) per pot of seedlings grown in experimental units consisting of three different planting compositions (i.e., *B. pendula* in monocultures, *P. sylvestris* in monocultures, or *B. pendula* and *P. sylvestris* in polyculture), four planting densities and four abiotic environmental conditions. Values for polycultures are the combined total mass of both species. Capital letters indicate significant difference between density treatments within each environment treatment, and lower case letters indicate significant differences between seedling composition means within each density x environment combination; ns indicates no significant difference between means (Tukey HSD, $\alpha = 0.05$). Data are means + SE.

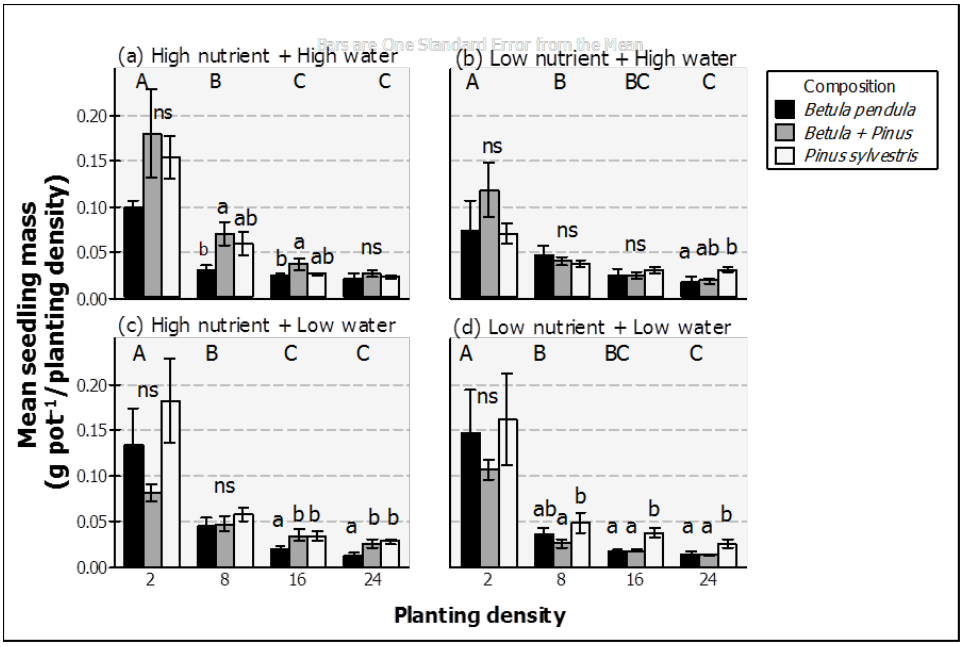

Figure 4. Mean seedling mass (total g pot^{-1} / total planting density) of seedlings grown in experimental units consisting of three different planting compositions (i.e., *B. pendula* in monocultures, *P. sylvestris* in monocultures, or *B. pendula* and *P. sylvestris* in polyculture), four planting densities and four abiotic environmental conditions. Values for polycultures are the combined total masses of both species / total planting density of the unit. Symbols and letters as for Figure 3.

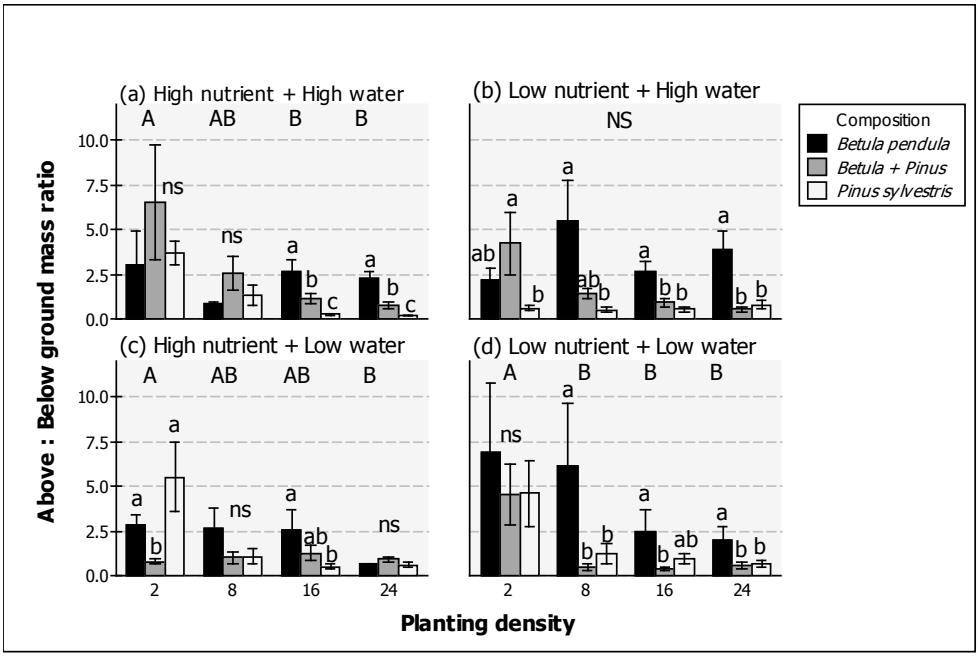

Figure 5. Above: below ground mass ratio of seedlings grown in experimental units consisting of three different planting compositions (i.e., *B. pendula* in monocultures, *P. sylvestris* in monocultures, or *B. pendula* and *P. sylvestris* in polyculture), four planting densities and four abiotic environmental conditions. Values for the polycultures are the combined totals of both species. Symbols and letters as for Figure 3.

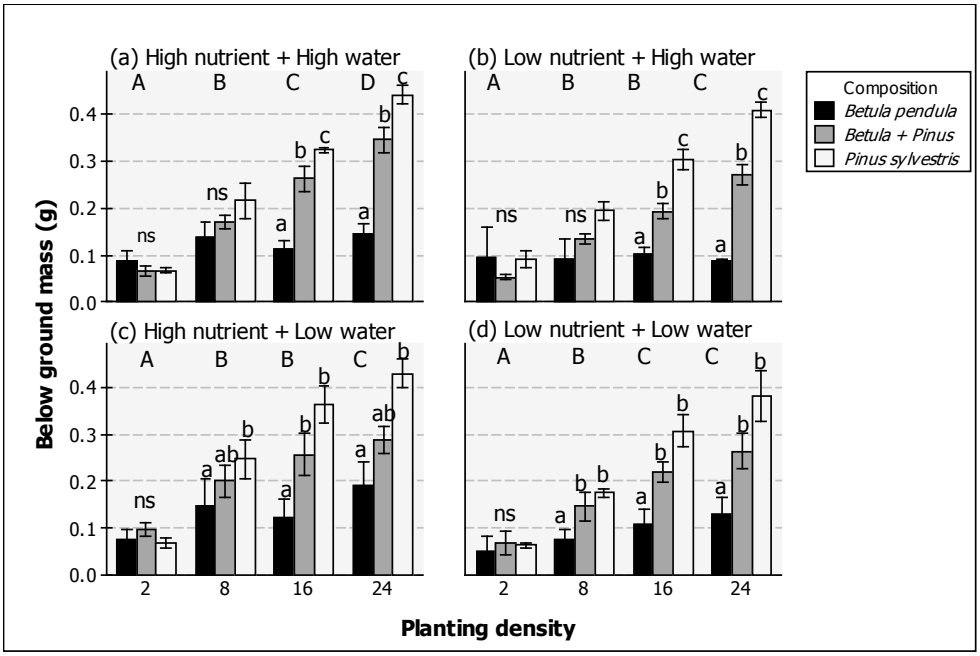

Figure 6. Total below ground mass per pot of seedlings grown in experimental units consisting of three different planting compositions (i.e., *B. pendula* in monocultures, *P. sylvestris* in monocultures, or *B. pendula* and *P. sylvestris* in polyculture), four planting densities and four abiotic environmental conditions. Values for the polycultures are the combined totals of both species. Symbols and letters as for Figure 3.

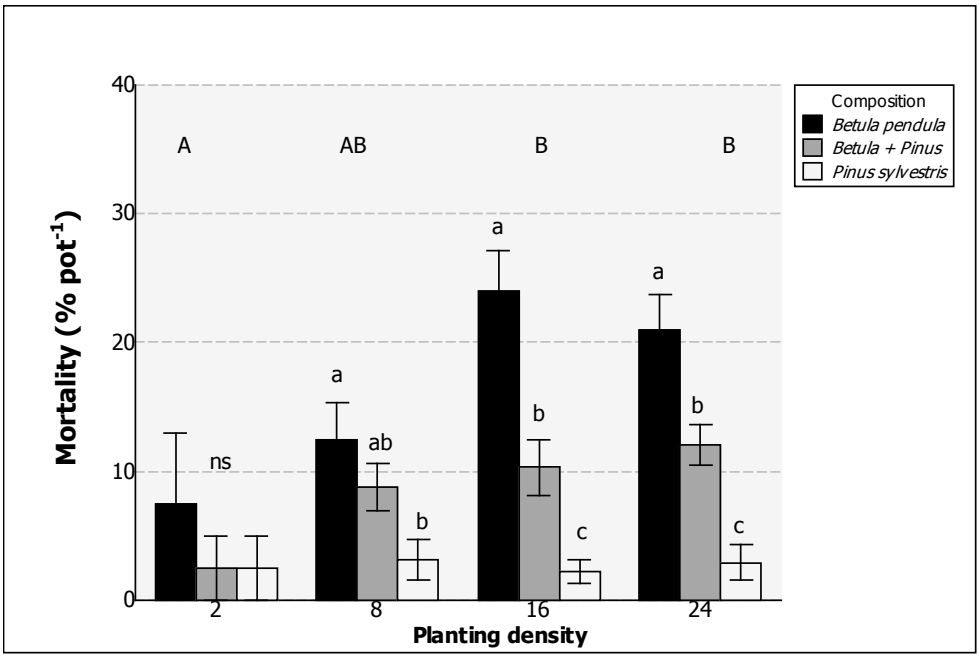

Figure 7. Total mortality (% pot^{-1}) consisting of three different planting compositions (i.e., *B. pendula* in monocultures, *P. sylvestris* in monocultures, or *B. pendula* and *P. sylvestris* in polyculture) and four planting densities Values for the polycultures are the combined total of both species. Symbols and letters as for Figure 3.

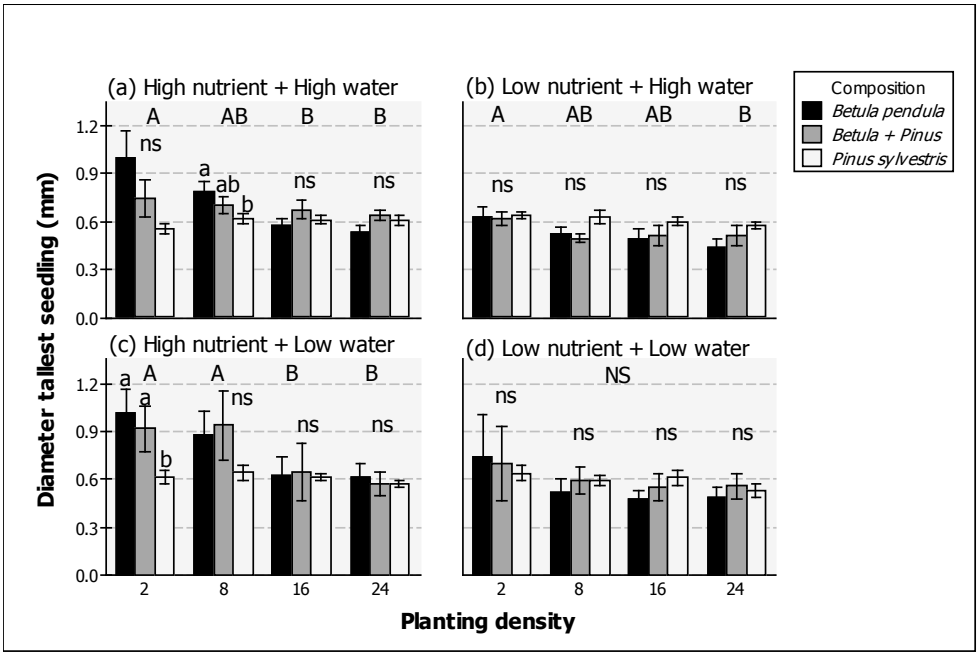

Figure 9. Diameter of the tallest seedling per pot, measured at the above: below ground interface grown in experimental units consisting of three different planting compositions (i.e., *B. pendula* in monocultures, *P. sylvestris* in monocultures, or *B. pendula* and *P. sylvestris* in polyculture), four planting densities and four abiotic environmental conditions. Values for polyculture are from the tallest seedling, regardless of species. Symbols and letters as for Figure 3.

3.2 Interactive Effects

The ANOVA testing for effects of planting composition, planting density and abiotic environmental conditions also revealed several two-way and three-way interactive effects between these experimental variables, suggesting that growth of tree seedlings in response to each of the main factors was dependent on the other experimental factors, i.e., planting composition, planting densities or environmental conditions (Table 1).

A significant interactive effect between the planting composition and planting density was found for the A:B ratio, below ground mass and seedling diameter, but not for the other variables (Table 1). For the A:B ratio, the interaction showed that the effect of density differed among planting compositions (Figure 5). At densities

greater than 2 seedlings per pot, the A:B ratio of *B. pendula* monocultures was either higher than that of the other two planting compositions or higher than that of the *P. sylvestris* monocultures. The A:B ratio was also the only response variable to be significantly impacted by an interactive effect between planting density and the abiotic environment treatments (Table 1). At conditions of high nutrient + high water and low nutrient + low water, the A:B ratio in general decreased with increasing density while in conditions of high nutrient + low water and low nutrient + high water the A:B ratio did not decline with increasing density (Figure 5). The change in A:B ratio under the effect of planting composition and density is also supported by the interactive effect of planting composition and planting density on below ground mass. A general trend of increasing below ground mass occurred when planting density was increased (Figure 6). This trend was strongest in *P. sylvestris* monocultures and weakest in *B. pendula* monocultures where the below ground mass showed only a marginal increase or remained relatively constant across all densities; this difference between planting compositions became more evident with increased density. Further, at low planting densities (e.g. 2 seedlings per pot) there were no statistical differences in below ground mass between planting compositions, while at higher planting densities (e.g. > 2 seedlings per pot) *B. pendula* monocultures consistently had the lowest below ground mass.

Moreover, there was an interactive effect between planting composition and density on seedling diameter. This effect resulted in *B. pendula* monocultures having the largest diameter at low planting densities, yet not significantly different from the mixed species planting composition, while *P. sylvestris* monocultures had the smallest diameter. The diameter of the *P. sylvestris*s in monocultures remained relatively constant with increased density. Both the mixed species planting com-

position and the *B. pendula* monocultures showed a decrease in diameter with increased planting density, however the reduction was weaker in the mixed species planting composition (Figure 9).

There was a significant interactive effect between planting composition and the abiotic environment on total mass, mean seedling mass, above ground mass and diameter, but not on the A:B ratio, below ground mass or mortality (Table 1). The mixed species planting composition had the greatest total mass under conditions of high nutrient+ high water, whereas *P. sylvestris* monocultures had the greatest total mass in conditions of low nutrient + low water (Figure 3). However, the mixed species planting composition was never significantly greater than both of the corresponding monocultures. In contrast to the mixed species treatment and *P. sylvestris* monocultures, the production of mass in the *B. pendula* monocultures remained relatively constant across contrasting nutrient and/or water conditions.

There was also a significant interactive effect of planting composition and abiotic environment on mean seedling mass (Figure 4). Under low nutrient conditions, all three planting compositions showed an overall lower mean seedling mass than in high nutrient conditions, with the lowest in *B. pendula* monocultures and strongest reduction in *P. sylvestris* monocultures. Under conditions of low water, the mean seedling mass of both monoculture planting compositions was greater than the mixed species planting composition and greater than in conditions of high water. The mean seedling mass in conditions of low nutrient + low water had similar but less extreme differences between planting compositions than that of the high nutrient + low water conditions. Both monocultures had marginally greater mean seedling mass than the mixed species composition in conditions of low nu-

trient + low water while the mixed species composition had a lower mean seedling mass (Figure 4).

The interactive effect of planting composition and abiotic environment on above ground mass (Table 1) resulted from that *B. pendula* monocultures responded differently than did both the *P. sylvestris* monocultures and mixed species planting compositions to environmental conditions (Figure 5). Although *B. pendula* monocultures had generally higher above ground mass than that of both *P. sylvestris* monocultures and the mixed species composition, it was lower at high nutrient + high water conditions (Figure 3), which was more evident in low densities. This result was further supported by the significant three-way interaction on above ground mass between planting composition, planting density and environment (Table 1). This showed that above ground yield differences among planting compositions was not only dependent on density, but also on environmental conditions. In low nutrient + low water conditions, above ground mass of *B. pendula* monocultures did not differ from the high nutrient + high water conditions. This was contrary to the mixed species planting composition. The mixed species composition had a lower above ground mass and the *P. sylvestris* monocultures a greater above ground mass in conditions of low nutrient + low water. These effects of the planting composition x abiotic environment effects were also shown to be density dependent (Table 1). In conditions of high nutrient + high water as well as low nutrient + high water *B. pendula* above ground mass increased with increasing density, where as in high nutrient + low water and low nutrient + low water conditions there was little to no change in above ground mass in *B. pendula* monocultures. This is different from *P. sylvestris* monocultures which showed decreasing above ground mass in high nutrient + high water conditions, relatively constant

above ground mass in low nutrient + high water and low nutrient + low water conditions and increasing above ground mass with increasing density in conditions of low nutrient + high water. Furthermore, as density increased, the mixed species composition showed relatively constant above ground mass in high nutrient + high water, low nutrient + high water and low nutrient + low water conditions, but increasing above ground mass in high nutrient + low water conditions.

The interactive effects of planting composition and abiotic environment on seedling diameter resulted from no change in the diameter of *P. sylvestris* monocultures across environments, which was contrary to the other planting compositions where the diameter was lower at lower nutrient conditions (Figure 9).

3.3 Mass-density relationship

All biomass variables changed with increasing density, showing at least that planting at densities of two seedlings per pot had significantly different effects from planting 24 seedlings per pot. Those variables representing total pot masses increased with the addition of more seedlings while the mean seedling mass, representing the weight of an individual within the pot, showed a negative relationship with planting density (Figure 9 and Table 2). The nature of this relationship, although untested and as seen in the intercept values and slopes, varied with planting composition and abiotic conditions. The strongest negative relationship between mean seedling mass and density occurred in high nutrient + high water conditions for the mixed species planting composition and the weakest relationship occurred in the low nutrient + high water conditions for *P. sylvestris* monocultures. Furthermore, each relationship presented different y-axis intercepts by species and by

abiotic condition. The greatest intercept was found in the mixed species planting composition in high nutrient + high water conditions while the lowest was in *B. pendula* monocultures in low nutrient + high water conditions. In high water conditions regardless of nutrient addition, the mixed species planting composition had the greatest intercept, while in low water conditions regardless of nutrient the *P. sylvestris* monocultures had the greatest intercept value (Table 2).

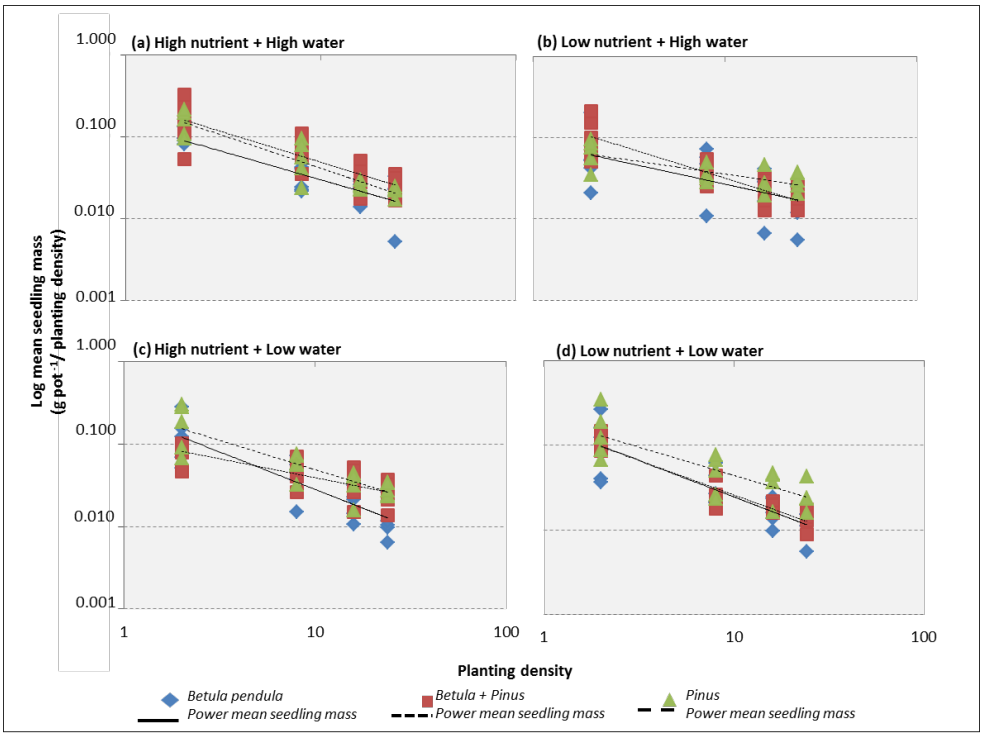

Figure 8. Mean seedling mass – density linear relationship for three different seedling planting compositions (i.e., *B. pendula* in monocultures, *P. sylvestris* in monocultures, or *B. pendula* and *P. sylvestris* in polyculture), four planting densities and four abiotic environmental conditions. Values for the polycultures are the total masses per pot of both species/ total planting density per pot. Values are plotted on a log-log scale of mean seedling mass and planting density with power regression. R^2-values, slopes and intercepts are found in Table 2.

Table 2. Power regression, slope intercept and R^2 values for the mass-density relationship of seedlings in three planting compositions (i.e., *B. pendula* in monocultures, *P. sylvestris* in monocultures, or *B. pendula* and *P. sylvestris* in polyculture), four planting densities and four abiotic environmental conditions. Values for the polycultures are the total masses per pot of both species/ total planting density per pot. Regression line expressed in Figure 10.

Treatment	Composition	*n*	Slope	Intercept	R^2
High nutrient + High water	*Betula pendula*	20	-0.0031	0.0811	0.5702
	Betula + Pinus	20	-0.0065	0.1585	0.4633
	Pinus sylvestris	20	-0.0056	0.1346	0.6078
Low nutrient + High water	*Betula pendula*	20	-0.0025	0.0720	0.2634
	Betula + Pinus	20	-0.0041	0.1006	0.4581
	Pinus sylvestris	20	-0.0016	0.0613	0.4143
High nutrient + Low water	*Betula pendula*	20	-0.0051	0.1174	0.4330
	Betula + Pinus	20	-0.0024	0.0774	0.5850
	Pinus sylvestris	20	-0.0063	0.1549	0.4399
Low nutrient + Low water	*Betula pendula*	20	-0.0048	0.1070	0.3654
	Betula + Pinus	20	-0.0037	0.0878	0.5898
	Pinus sylvestris	20	-0.0054	0.1369	0.3583

4 Discussion

The understanding of how stand development is influenced by planting composition, planting density and contrasting environments has recently become a popular topic in forest ecology and silviculture (Condes et al., 2013). In general it is known that all three factors, influence the yield of mature stands and are of key importance for forestry practitioners in stand management (Hyink and Zedaker, 1987). Of late, much consideration has been given to the potential benefits of mixed stands over to monospecies stands in regards to productivity, resistance to environmental change and benefits of species diversity. While most studies have focused on mature mid-rotational stands and the effects of these three factors on stand productivity (e.g. Kelty (2006), Condes et al. (2013), Pretzsch et al. (2010), Pretzsch et al. (2012), it is expected that these will also impact the growth and yield of seedlings. The goal of this study was to contribute to the understanding of how these factors influence growth of *Betula pendula* and *Pinus sylvestris* seedlings. My study showed that planting composition, planting density and abiotic environment all have significant effects on various aspects of yield in *B. pendula* and *P. sylvestris* seedlings. Furthermore my study showed that these factors can have significant interactive effects, showing that mixed tree seedling communities may show higher yield than monospecific seedling communities, but only at par-

ticular combinations of species composition, planting density and environmental conditions. Although the yield sometimes was greatest in mixtures, it was never significantly greater than both monocultures, and therefore these conclusions should be treated with caution. Further, this work also supports the argument that the impacts of planting density and environments on yield and the characteristics of yield may differ for different communities.

In response to my first question I found that planting composition and planting density, as well as the interaction between these, had significant effects on seedling yield. After 10 weeks of growth, significant differences in total seedling mass, mean seedling mass, A:B ratios, below ground mass and mortality were found among all three planting compositions. This is consistent with current knowledge on species specific characteristics and prediction of yield in mature stands, with conifers and angiosperms (here *P. sylvestris* and *B. pendula*) having differences in development, morphology and survival (Carnicer et al., 2013, Drobyshev et al., 2013, Ostonen et al., 2007), and with the expectation that a higher planting density will result in higher yield per area (Li et al., 2013). While differences between the two monocultures were as expected, my results showed that *P. sylvestris* seedlings produced a higher total yield than *B. pendula* for 5 out of the 20 density x treatment combinations, mostly at high densities. Interestingly, the yield of mixed species treatments did exceed the yield of both monocultures under some conditions, mostly at mid densities and in the richest environment. While never significantly greater, this suggests that after more than 10 weeks of growth, overyielding may occur in specific combinations of planting density and environment.

The greater mortality in the *B. pendula* monocultures is similar to the findings of Dalling and Hubbell (2002), who found higher mortality rates in the fastest-

growing pioneer species. Furthermore, the differences in total mass among planting compositions are likely to be attributable the differences in below ground mass (indicative of root growth) of *P. sylvestris* and *B. pendula* seedlings. In accordance with previous studies of growth along density gradients, the significantly greater biomass in the higher densities is concurrent with findings of Li et al. (2013). They showed that greater biomass was produced from higher sowing densities; which supports the possibility that the effect of self-thinning was not yet great enough to overcome the additional mass added by individuals alone. Likewise, the decrease in individual seedling mass and seedling diameter with increasing density supports the basis of density dependent growth and growth limitation prior to self-thinning caused mortality (Deng et al., 2012, Li et al., 2013). With only minimal changes in characteristics of yield occurring when density was increased from 8 to 24 seedlings per pot it is possible that the seedlings approached a critical density at less than 8 seedlings per pot, or is found at a density greater than 24 seedlings per pot. At that density the seedlings would have been faced with a trade-off between growth and survival, resulting in no, or negative change in yield but maintained survival. Further, the low increase in mortality with increased density suggests the actual self-thinning line was not reached. This is in agreement with previous studies on size and growth allometry showing decreased growth with increased density only once a critical density has been reached and density dependent effects become a more important parameter for growth while mortality occurs once this threshold line is surpassed (Niklas et al., 2003, Kelty, 2006). In addition, my study showed that after 10 weeks of growth seedlings in the mixed species planting composition were no less susceptible to the effects of increased density on yield than seedlings in monocultures. However, the characteristics of

the mass may vary between monocultures and mixture with increasing density, as revealed by the significant interactive effect of planting composition and density on A:B ratio, below ground mass and stem diameter. The increases in total yield with increasing density for all planting compositions are also supported by the inconclusive and debated findings on the suitability of the -3/2 slope of the density-yield relationship as was proposed by Yoda et al. (1963). The mean seedling mass- density relationship was negative for all my planting communities, and the coefficient ranged between -0.0016 and -0.0065 (Table 2). If self-thinning did occur during this artificial period it would support the argument that the self-thinning line varies among different planting compositions and that the coefficient -3/2 is not a constant among tree species (Charru et al., 2012).

In response to my second question I found that planting density impacts on final yield, but that it also differs under contrasting abiotic conditions. This finding is consistent with previous literature on seedlings and mature stands (Li et al., 2013, Deng et al., 2012, Condes et al., 2013, He and Duncan, 2000). My results show that the effect of planting density on seedling yield is also dependent on the abiotic environment regardless of whether the stand is composed of monocultures or species mixtures. Conversely, the interaction of planting density effects and abiotic environment effects had fewer statistically significant effects than each factor in isolation, and was only significant for the A:B ratio. This is concurrent with the suggestion of optimal partitioning models in that plants should adjust partitioning to minimize imbalance of resources (McConnaughay and Coleman, 1999). Such adaptations in partitioning could therefore result in changes in A:B ratio, yet possibly not total mass or individual mass. For experimental units where the environment did have an effect, the difference between high and low water conditions

was relatively low, implying that the water conditions in this study had a lower importance than nutrient conditions for the growth and development of seedlings. The greater importance of nutrient conditions is compatible with the current knowledge on growth limitation in boreal forests. Plant reactions to change in nutrient well as the root response to adverse conditions can result in the changes seen in A:B ratio (Tamm, 1991, Ostonen et al., 2007). Contrary to the belief that increased nutrient would allow increased growth at higher densities, my results rather suggest that nutrients have limited impact on seedling yield, and yield characteristics at high density. This is concurrent with the findings of Walker and Chapin (1986) who found competition and facilitation to have a greater influence on the development of seedlings than abiotic conditions alone, and that facilitative processes may enable plants to overcome resource limitation.

In response to my third question I found that the total yield and characteristics of the yield (e.g. A:B ratio and diameter) were influenced by both composition and environmental conditions. Again, this is in line with current knowledge on morphological and physiological differences between mature *B. pendula* and *P. sylvestris*, with *B. pendula* showing greater growth in higher nutrient conditions while *P. sylvestris* is able to support higher growth under poorer conditions, notably drier situations. Specifically I found that *P. sylvestris* outperformed both the *B. pendula* monoculture and the mixed species planting composition in conditions of high nutrient + low water and conditions of low nutrient + low water. This was especially observed when data was presented as log mean seedling mass- log density relationships. Furthermore, the observation of mixed species planting composition outperforming both *B. pendula* and *P. sylvestris* monocultures only in high nutrient + high water conditions is consistent with previous findings on yield in

mixed stands and findings that the outcome of overyielding or underyielding varies with site conditions (Pretzsch et al., 2012, Hynynen et al., 2011). Similar to my results, Hynynen et al. (2011) also found that favorable conditions increased the performance of the mixed stands. In resource rich environments it appears that seedling mixtures are better able to use the available resources with complementary niches, as *B. pendula* and *P. sylvestris* do not have directly overlapping needs (Pretzsch et al., 2012). This was noted in particular by a difference in root growth when plants were harvested. *B. pendula* roots remained fine and within the upper half of the growing medium, while the roots of *P. sylvestris* seedlings became associated with mychorizae and extended throughout the entire growing medium. This was further indicative of different resource demands of the two species. It is also possible that *B. pendula* and *P. sylvestris* seedlings have a facilitative relationship in which the growth one seedling enhances the growth of the other as suggested to occur in mixed stands of mature trees by Kelty (1992). Here the mixed stands presented greater total mass and larger mean seedling masses in conditions of high nutrient and high water, however, this potential overyielding effect of the mixed species composition was not maintained in conditions of low nutrient, low water or both low nutrient and low water. Furthermore, my results support the argument that the self-thinning law and the -3/4 coefficient is again not constant across environments and species, and may differ between young and mature stands.

While significant differences occurred in the response variables as a result of the imposed treatments, there is great potential for other confounding factors to be impacting on the seedling yield and yield characteristics in this study. For example it was also shown from the GLM results (Table 1) that blocking treatment had a

significant effect. The blocking aspect of this experimental design was primarily established to avoid the bias in environment setting within the greenhouse environment. As there was no significant effect of blocking on mortality, the effects of blocking in this experiment are to be considered as noise. The significant effect observed from blocking is probably due to unintentional differences in soil compaction among blocks. Despite careful placement of growing material into the pots I cannot rule out that the growing medium was not compacted to different levels, and thus had contributed to the blocking effect. Another important aspect in this study is time period allotted for seedling growth under the treatments. As indicated by the bud set by some *P. sylvestris* seedlings the time given under the set conditions was approximately one growing season (Hurme et al., 1997, Salminen and Jalkanen, 2007). It is possible that changing the length of the growing season would also impact the yield of seedlings; exposing seedlings to the treatments longer and allowing more time for differentiation based on the treatment effects to develop. Furthermore there was a distinct change in coloration of some seedlings, *B. pendula* becoming redder and *P. sylvestris* which faded from a dark green to a pale brighter green. The change in color observed in the *B. pendula* could be attributed to various stressors such as wounding, UV-B radiation, high light in cold temperatures, transplant stress or nutrient deficiency and the resulting production of anthocyanins (Manetas, 2006). The paler green colors of some *P. sylvestris* seedlings in low nutrient conditions is indicative of the soil nitrogen content being lower (Mandre et al., 2010) than in the high nutrient environments. This indicates that the soil nutrient levels differed among treatments, however further analysis is needed to confirm the extent of the difference in soil fertility, (i.e. N concentrations). Further, I observed that experimental units treated with low nutrients had a

higher abundance of bryophytes. While this was unintentional, the finding of more weedy species in the low nutrient environments where growing medium had a greater concentration of natural soil confirms there was a difference in soil environments. In future studies investigation into the yield of seedling in mixtures and monocultures should consider total mass as determined by the sum of individual masses within each pot wherever possible. By using the individual masses in the mixed species composition it would be possible to determine if one species is outcompeting the other by any potential change in the proportion of the planting composition. Additionally, future studies should continue with the statistical analysis and fitting of self-thinning curves for seedlings, following the procedure as suggested by Weller (1987) to avoid spurious correlations and to definitively compare the coefficients developed from seedlings under these treatments to the global -3/2 coefficient proposed by Yoda et al.

In conclusion, this study addresses the current lack of knowledge on yield in seedlings under various growing conditions. I have shown that the yield of *B. pendula* and *P. sylvestris* seedling monocultures differ from each other, as well as from a two species mixture, and that the magnitude of the differences are dependent on both planting density and abiotic condition as well as the interactions of these parameters. While it is not possible to conclude one given combination of factors that results in the best seedling performance this study provides insight to the knowledge required by forest managers to successfully obtain the greatest seedling performance.

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